# 26

# Nutritional Ecology of Fungus-Feeding Arthropods

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26.1 Introduction
26.2 Natural History
  26.2.1 Arthropods Associated with Macroscopic Spore-Producing Structures
  26.2.2 Arthropods Associated with Vegetative Tissues and Microscopic Spore-Producing Structures
26.3 Behavioral Aspects
  26.3.1 Allelochemicals from Mushrooms
  26.3.2 Selection of Nonfungal Substrates on the Basis of Fungal Associates
26.4 Physiological Aspects
  26.4.1 Digestive Capabilities of Fungivores
  26.4.2 Fungal Toxins and Their Effects on Fungivores
  26.4.3 Substrate Modification by Fungi
26.5 Ecological and Evolutionary Aspects
  26.5.1 Host Specificity among Invertebrates That Feed on Sporocarps
  26.5.2 Host Specificity among Invertebrates That Feed on Materials Colonized by Fungi
26.6 Conclusions
References

## 26.1 INTRODUCTION

Fungal tissue is the food of many invertebrates representing phylogenetically and ecologically diverse taxa. The study of fungivory (or mycophagy) provides an opportunity to address many evolutionary, ecological, physiological, and biochemical questions that have been the focus of much recent research on herbivory. For example, do patterns of host specificity reflect associations resulting from mutual descent (coevolution) or from recent colonization events? What factors select for specialists with narrow host ranges versus generalists with broad host ranges? To what extent does the relative unpredictability of fungi make them "unapparent" to potential fungivores, and what are the ecological and evolutionary consequences of this unpredictability? To what extent does the diverse array of chemicals present in fungi serve to protect them from potential fungivores, and what are the mechanisms by which fungus feeders cope with potential toxins? How do mycophagous species find their preferred hosts, and what are the indicators of acceptability? How effectively is fungal tissue assimilated, and what are the determinants of nutrient quality? In this chapter we review investigations of arthropod–fungus interactions that bear on these questions. We have tried to relate our discussions to the conceptual framework provided by recent research on insect herbivory.

Many arthropod inhabitants of the fruiting bodies of higher macrofungi (Ascomycetes and Basidiomycetes) are obligate fungivores. There are also many species of invertebrates that feed exclusively or predominantly on fungal tissue by grazing selectively on the vegetative portions and on the microscopic reproductive structures of filamentous fungi that permeate the habitat in which they live. Still other species ingest relatively small quantities of fungal tissue along with larger amounts of other materials, most often the substrate on which the fungus is growing. Anderson and Cargill (Chapter 30), Haack and Slansky (Chapter 15), Hanski (Chapter 28), Lawrey (Chapter 6), Stradling (Chapter 31), Waller and La Fage (Chapter 16), and Werner and Dindal (Chapter 27) discuss the biology and nutritional ecology of several such feeding guilds. In our chapter we consider the implications of mycophagy both to those species that feed largely or exclusively on fungal tissue and to those that consume smaller quantities of fungal tissue along with other materials. However, to minimize overlap with other chapters, our discussion of this latter group will focus on studies that define the special significance of the fungal component of the diet, with special emphasis on the relevance of the results to the questions posed in the previous paragraph.

## 26.2 NATURAL HISTORY

### 26.2.1 Arthropods Associated with Macroscopic Spore-Producing Structures

The fruiting bodies of higher macrofungi provide food and shelter for many species of arthropods. Mites, springtails, thrips, beetles, and fly larvae are the most frequent and abundant associates of woody fungi (Scheerpeltz and Höfler, 1948; Benick, 1952; Rehfous, 1955; Graves, 1960; Pielou, 1966; Pielou and Verma, 1968; Matthewman and Pielou, 1971; Ackerman and Shenefelt, 1973; Gilbertson, 1984; OConnor, 1984), and fly larvae dominate the fauna of the shorter lived fleshy fungi and those woody fungi with fruiting bodies that persist for only 2–3 weeks (Scheerpeltz and Höfler, 1948; Buxton, 1960; Paviour-Smith, 1960a; Hackman and Meinander, 1979; Bruns, 1984). Blisters and cankers, formed on plants in response to infection by parasitic fungi such as rusts and smuts, are exploited as food by a number of insects (Mutuura and Monroe, 1969; Coulson and Franklin, 1970; Powell, 1971; Furniss et al., 1972; Wheeler, 1972; Wong, 1972). Of the numerous species of arthropods that may be associated with the sporocarps (macroscopic fungal fruiting bodies) of a given fungal species, only a few are likely to be true mycetobionts (i.e., obligate fungus feeders that spend their entire lives or an entire developmental stage in the fungus). Many more are nonobligatory associates, such as polyphagous species, predators, and casual visitors from the forest floor community. The natural history of insect–fungus associations is described in widely dispersed articles in entomological, mycological, and ecological journals. Wheeler and Blackwell (1984) provide access to this extensive body of literature.

Although the sporocarps of a given fungus species may support a large number of arthropod species in some particular geographic area, in any single sporocarp the number of species and individuals is small, and the population structure is unpredictable from sporocarp to sporocarp. Pielou and Verma (1968) reported that although 257 species of insects and mites have been collected from the birch bracket fungus *Polyporus betulinus,* the number of species on any given sporocarp ranged from 0 to 13, with an average of only 0.7 in young sporocarps and 2.9 in old sporocarps. Thirty-eight percent of the sporocarps were not colonized (Pielou, 1966). In *Fomes fomentarius,* a fungus that persists for a shorter time than *P. betulinus,* 152 species were collected from the fruiting bodies, whereas the number per sporocarp ranged from 0 to 5 with a mean of 0.5. Two thirds of the sporocarps were not colonized (Pielou and Matthewman, 1966; Matthewman and Pielou, 1971). Pielou and Pielou (1968) have also noted that although many species of arthropods may be associated with a given species of fungus, only a few species occur on a large fraction of sporocarps that have been colonized. Most of the arthropod species that associate with fungal fruiting bodies are of infrequent occurrence.

The arthropod community associated with a given fungus species changes as the sporocarps mature and ultimately decay (Park, 1931; Scheerpeltz and Höfler, 1948; Benick, 1952; Rehfous, 1955; Graves, 1960; Paviour–Smith, 1960b; Dajoz, 1966; Matthewman and Pielou, 1971; Ackerman and Shenefelt, 1973). Whether the change in species composition is a true succession or only a seral increase in number of species is not entirely clear. The largest number of species is found on sporocarps at advanced stages of decay, at which time the community of associated arthropods closely resembles the more general community typical of the forest floor.

Although in the majority of cases it is not known what part of a fruiting body is actually being eaten by a mycophagous species, it is clear that there are differences in the ways that some species use the resources within a sporocarp. Some species restrict themselves to specific tissue layers, and others feed throughout the sporocarp. Still others are specialized spore feeders (Park, 1931; Park et al., 1931; Dybas, 1956; Liles, 1956; Graves, 1960; Paviour–Smith, 1965; Lawrence, 1973; Ananthakrishnan, 1979; Ashe, 1984; Bruns, 1984; Newton, 1984).

### 26.2.2 Arthropods Associated with Vegetative Tissues and Microscopic Spore-Producing Structures

Arthropods are common in a number of habitats that include decaying plant tissues permeated by the vegetative and reproductive structures of filamentous fungi. Arthropods that inhabit soil, detritus, decaying wood, and herbivore dung are all potential fungus feeders. Millipedes, isopods, mites, springtails, thrips, beetles, and fly larvae are common litter inhabitants in terrestrial systems, and amphipods, stonefly nymphs, and the larvae of caddisflies, crane flies, black flies, and mosquitoes are common aquatic detritus feeders. Mites, springtails, thrips, termites, and beetles are the most common invertebrates encountered under bark or in rotting wood, and mites, springtails, beetles, and fly larvae are most abundant in dung. Analyses of gut contents have clearly established that many of these species consume fungal hyphae and spores, often together with other materials (Dawson, 1965; Freeman, 1967; Sands, 1969; Anderson and Healey, 1972; Lindquist, 1975; Swift et al., 1979; Ashe, 1984; Blackwell, 1984; Crowson, 1984; Gilbertson, 1984; Newton, 1984; OConnor, 1984; Steiner, 1984; Wheeler, 1984). The most nutritious component of litter is the associated bacterial and fungal biomass, and numerous studies have demonstrated that many detritus- and wood-feeding invertebrates have a preference for, and enhanced growth on, substrates that support a rich culture of microorganisms, especially fungi (Cummins and Klug, 1979; Bärlocher and Kendrick, 1981; Martin and Kukor, 1984).

Fermenting fruits and plant exudates are other potential resources in which arthropods are likely to encounter fungi, especially yeasts, which are a single-cell growth form of certain fungi. The drosophilids that exploit fermenting plant materials and the beetles found in sap flows are dependent on the yeasts present in their food (Starmer, 1981; Begon, 1982; Crowson, 1984).

Though many detritus-, wood-, and dung-feeding insects exploit the fungi that normally grow on these substrates, there are other insects that actively culture the fungi that they ingest. These mutualistic associations of insects and fungi provide several spectacular examples of complex, coevolved symbioses. Fungus-growing termites (Macrotermitinae; Sands, 1969; Heim, 1977), siricid wood wasps (Siricidae and Xiphydriidae; Francke–Grosmann, 1967), and ambrosia beetles (Scolytidae, Platypodidae, and Ipidae; Francke–Grosmann, 1967; Barras and Perry, 1975) culture symbiotic fungi on wood and ingest mixtures of fungus and woody substrate. Fungus-growing ants culture their symbiotic fungi on freshly cut leaves, plant debris, insect feces, or insect exoskeletons (Weber, 1972). The fungal tissue is the exclusive food of the ant larvae and a minor component of the diet of adult workers (Quinlan and Cherrett, 1979).

## 26.3 BEHAVIORAL ASPECTS

### 26.3.1 Allelochemicals from Mushrooms

A wide variety of secondary metabolites including polyenes, polyacetylenes, terpenes, furans, pyrones, depsides, tropolones, isocoumarins, phenols, quinones, anthraquinones, melanins, nonprotein amino acids, alkaloids, and peptides occur in fungi (Miller, 1961; Birkinshaw, 1965; Arpin and Fiasson, 1971; Turner, 1971; Arpin and Kuhner, 1977; Bresinsky and Besl, 1979; Turner and Aldridge, 1983). It seems clear that many of these substances must play an important role in the location, acceptance, avoidance, or rejection of mushrooms by fungivorous arthropods in search of feeding or oviposition sites. However, there are very few studies of chemicals from mushrooms that influence insect behavior.

1,3-Diolein has been identified as a house fly attractant in the mushroom *Amanita muscaria* (Muto et al., 1968). Both 1- and 2-oleoylglycerol, which were not detected in this mushroom, are more attractive to the flies than diolein. It is well known that flies are attracted to the foul-smelling slime produced by the basidiocarps of the stinkhorn fungi (Phallales) and to the nectarlike secretions produced by the pycnidial stage of many rust fungi, but the chemicals responsible for attraction have not been identified. Flies attracted to these secretions act as spore dispersal agents. Fungal extracts containing volatile carbonyl compounds and eight-carbon alcohols are also attractive to flies (Pyysalo, 1975; Hackman and Meinander, 1979). *Cis*- and *trans*-octa-1,5-dien-3-ol, which occur together in many fungi, are attractants for the mycophagous mite *Tyrophagus putrescentiae* (Vanhaelen et al., 1980). Fungal metabolites have also been implicated as attractants of parasitoids of mycophagous insects. Acetaldehyde, ethanol, and acetic acid are attractants for *Biosteres longicaudatus*, a parasitoid of tephritid fruit fly larvae which are often found in rotting fruit (Greany et al., 1977), and several hymenopterous parasitoids of the wood wasp *Sirex noctilio* are attracted by metabolites of the wasp's symbiotic fungus (Madden, 1968).

### 26.3.2 Selection of Nonfungal Substrates on the Basis of Fungal Associates

It is widely recognized that food selection by both terrestrial and aquatic detritivores is strongly influenced by the microorganisms associated with decaying leaves. Amphipods (Bärlocher and Kendrick, 1973a,b; Rossi, 1984), isopods (Rossi, 1984), ephemeropteran nymphs (Basset and Rossi, 1982b), and trichopteran larvae (Suberkropp et al., 1983; Arsuffi and Suberkropp, 1984, 1985; Suberkropp and Arsuffi, 1984) prefer leaves colonized by fungi to ones not colonized and are able to distinguish between different fungi and between leaves colonized by different fungi. It seems reasonable to assume that chemicals produced by the fungi or liberated from the substrate under the influence of fungal metabolism are among the factors that influence detritivore feeding behavior, but little progress has been made in identifying the substances involved. Cinnamic acid (Valiela et al., 1979) and ferulic acid (Valiela and Rietsma, 1984) reduce the palatability of detritus of the salt-marsh grass *Spartina alterniflora* to the snail *Melampus bidentalus,* but these phenolic acids are secondary metabolites from the plant tissue, not products of fungal metabolism.

Wood-rotting basidiomycetes influence the acceptability and suitability of wood to certain termite species and produce chemical substances that elicit behavioral responses by the termites (Amburgey, 1979; Gilbertson, 1984). The termite attractant from the fungus *Lenzites trabea* is similar or identical to (Z,Z,E)-3,6,8-dodecatriene-1-ol, which is the trail-following pheromone produced by the termites *Reticulitermes flavipes* and *R. virginicus* (Smythe et al., 1967; Matsumura et al., 1969). Aggregation by the confused flour beetle *Tribolium confusum* is elicited by mycelial constituents, possibly triglycerides, of the fungus *Nigrosporum sphaerica* (Starratt and Loschiavo, 1971). Drosophilids exploit a variety of natural substrates, including decaying plant tissue, slime fluxes, and mushrooms, and the suitability and acceptability of a habitat for feeding or oviposition are strongly influenced by the abundant yeast microflora associated with these substrates (Kimura, 1976, 1980; Starmer, 1981, 1982; Vacek, 1982). In no case have the chemicals responsible for selectivity been characterized.

## 26.4 PHYSIOLOGICAL ASPECTS

### 26.4.1 Digestive Capabilities of Fungivores

Although fungi have been compared to high-grade vegetables in their nutritive potential (Crisan and Sands, 1978), fungal tissue is qualitatively very different from vascular plant tissue (see Martin, 1979, for a review of the chemical composition of fungal tissue). Fungi contain unique structural and storage polymers and lack many of the biopolymers that are characteristic of higher plants, such as lignin, cellulose, and pectin. Thus, to maximize digestive efficiency, mycophagous and phytophagous insects would require different digestive capabilities. A study of the digestive enzymes of eleven species of fungus-feeding beetles (Martin et al., 1981b) has shown that these species are able to digest $\beta$-(1,3)- and $\alpha$-(1,4)-glucans, which are the major cell wall and storage polysaccharides of higher fungi, but are unable to digest cellulose, hemicellulose, or pectin. In addition, low levels of chitinolytic enzymes were found in gut fluid of beetles that inhabited woody polypores.

Surveys of the digestive enzymes of detritivores suggest a greater capacity to utilize fungal polysaccharides than plant polysaccharides (Nielsen, 1962, 1963; Bjarnov, 1972; Martin et al., 1980, 1981a,c). Analyses of the digestive and assimilative efficiencies of detritivores corroborate the enzymatic studies. Values for approximate digestibility (AD) are exceedingly low (6–35%) for detritus-fed animals, whereas values range from 42 to 97% when animals are fed only the microbial component of the detritus (Berrie, 1976; Cummins and Klug, 1979). Bärlocher and Kendrick's (1973b, 1975a, 1981) studies of the aquatic amphipod *Gammarus pseudolimnaeus* provide a convincing demonstration of the potential nutritional value of fungi to a detritivore. On a diet of autumn-shed leaves, *Gammarus* assimilates only 10–20% of the calories, dry matter, and protein in the leaves. However, when reared on the decay fungi isolated from these leaves, *Gammarus* assimilates 43–76% of the dry matter and 73–96% of the fungal protein. Although these studies demonstrate that detritus feeders can make efficient use of the relatively limited fungal biomass in their diets, they do not necessarily imply that the assimilation of more refractile substrate constituents, inefficient though it may be, is unimportant to the nutritional well-being of such species.

### 26.4.2 Fungal Toxins and Their Effects on Fungivores

As indicated in Section 26.3.1, fungi contain a wide variety of secondary metabolites. Many of these compounds are known toxins, inhibitors, or growth regulators of bacteria, plants, or vertebrates, but little is known of their effects on insects or other arthropods. There is no doubt that many of these substances are potentially harmful to the arthropods that might consume them, and their presence presents a challenge to the detoxification capacities of potential consumers. The cyclic peptides amanitin and phalloidin are among the best-studied fungal toxins (Wieland and Faulstich, 1978). Amanitins comprise up to 0.7% of the dry matter in the sporocarps of several species of *Amanita* and owe their toxicity to a specific inhibition of eukaryotic DNA-dependent RNA polymerase II (Faulstich et al., 1974; Faulstich, 1980). Several species of mycophagous *Drosophila* regularly use amanitin-containing mushrooms as breeding sites (Jaenike, 1978b; Jaenike and Selander, 1979; Jaenike et al., 1983). Larvae of these flies ingest quantities of $\alpha$-amanitin that are lethal to nonmycophagous species of *Drosophila*. The basis for this amanitin tolerance has not been determined, but a structurally altered RNA polymerase is apparently not involved. Several species of gyrophaenine staphylinid beetles (Ashe, 1984) and a eupodid mite (OConnor, 1984) are also known to feed in amanitin-containing sporocarps, but nothing is known of the basis for their abilities to tolerate or detoxify these peptides.

Another group of insecticidal compounds isolated from sporocarps of *Amanita muscaria* and *A. pantherina* is represented by the amino acid analogues ibotenic acid and muscimol (Takemoto and Nakajima, 1964b; Bowden et al., 1965; Wieland, 1968). A structurally related compound, tricholomic acid, occurs in several species of *Tricholoma* (Takemoto and Nakajima, 1964a; Chilton, 1978). Although the toxicity of these mushrooms to muscid flies is well known (Catalfomo and Eugster, 1970), no feeding studies have been conducted using naturally occurring insect associates of these fungi. Muscimol has been shown to be a potent antifeedant to opossums (Camazine et al., 1983). Clitocine, a nucleoside isolated from the mushroom *Clitocybe inversa*, has strong growth inhibiting activity against the pink bollworm *Pectinophora gossypiella* (Kubo et al., 1986).

In a comprehensive study of the insect associates of the Boletales in the upper midwestern United States, Bruns (1984) noted that fresh sporocarps of *Strobilomyces floccopus* are totally devoid of insects. L-dopa has been isolated from this mushroom (Steglich and Esser, 1973), and it may play the same antifeedant role in this fungus as it does in legume seeds (Rehr et al., 1973). The absence of dipteran larvae in *Paxillus atrotomentosus* and various *Dermocybe* species has been attributed to growth-retarding toxins, possibly anthraquinone pigments in the case of *Dermocybe* (Besl and Blumreisinger, 1983).

Species of *Aspergillus, Penicillium,* and *Fusarium* that occur on stored grain are known to produce a variety of toxic metabolites. These mycotoxins, which are known primarily from their devastating impact on vertebrate consumers (Ciegler, 1975; Uraguchi and Yamazaki, 1978), have adverse effects on growth and development in several grain-infesting insects (Wright et al., 1980; Davis, 1982; Wright, 1982; Wilson et al., 1984). The effects of the toxins vary considerably with insect species, developmental stage, and environmental conditions, and overall toxicity is more pronounced when the insects are on a suboptimal diet (Wright and Harein, 1982). There is a growing body of evidence that interactions between many grasses and their herbivores may be mediated by endophytic fungi (Balansiae, Clavicipitaceae), which produce alkaloids that may act as toxins or deterrents (Clay et al., 1985).

### 26.4.3 Substrate Modification by Fungi

The value of fungal tissue to an arthropod that consumes it may reside as much in the metabolic characteristics of the fungus as it does in its caloric content. Owing to their branched tubular mode of growth, their multiple growing tips, their ability to penetrate and permeate a substrate, and their secretion of hydrolytic enzymes, filamentous fungi can bring about marked changes in the physical and chemical composition of a substrate. These changes can increase the acceptability, attractiveness, palatability, and digestibility of a potential food item.

Wood is a resource in which insect invasion is often dependent on prior fungal attack. The heartwood of many tree species contains an abundance of secondary metabolites, including alkaloids, terpenes, and phenols (Highley and Kirk, 1979), which can make the wood unacceptable to xylophagous insects. Decay of this wood by heart rot fungi can render these allelopathic compounds innocuous. For example, Becker (1975) found that the termite *Coptotermes sjostedti* would accept the highly resistant heartwood of the African tree *Autranella congolensis* only after fungal decay. Similarly, sound heartwood of *Pinus caribaea* has a high resin and turpentine content and is unacceptable to *C. niger*. However, when decayed by the brown rot fungus *Lentinus pallidus*, the heartwood is consumed by the termites and is accepted as a nesting site (Williams, 1965).

Another illustration of fungal conditioning of a substrate prior to insect attack is provided by the interaction between the mountain pine beetle *Dendroctonus ponderosae* and blue-stain fungi. Susceptible stems of lodgepole pine are inoculated with insect-borne fungal propagules during the beetle's initial feeding. The successful establishment of the beetle, however, depends on the ability of the fungus to suppress the tree's defensive response, killing sufficient tissue to permit the beetle to establish brood galleries (Safranyik et al., 1975). Blue-stain fungi play a similar role in the colonization of their hosts by several other species of bark beetles (Francke-Grosmann, 1967).

The ability of *Drosophila mojavensis* to breed successfully in one of its favored habitats, the decaying stems of organ-pipe cactus, also depends on the metabolic activity of a fungal colonizer of this habitat. Organ-pipe cactus tissue contains up to 15% of its dry weight as lipids, composed of unusual fatty acid esters of sterol diols and triterpene diols (Kircher, 1980). Starmer (1982) has shown that the free fatty acids liberated during bacterial necrosis of cactus tissue are inhibitory to the growth of *D. mojavensis*. However, the fly will develop successfully when lipolytic yeasts are present. The yeasts utilize the lipids and fatty acids of organ-pipe cactus as their carbon and energy source and, in so doing, detoxify the cactus tissue for *D. mojavensis*.

Another way in which fungal metabolic activities can be important to mycophagous arthropods is through substrate enrichment. Fungi concentrate biologically important nutrients such as nitrogen, phosphorus, and potassium from extremely dilute substrates such as wood, soil, and leaf litter (Remacle, 1981; Swift and Boddy, 1984). The importance of this concentrating capacity is illustrated by Merrill and Cowling's (1966) demonstration that an insect would have to consume 36.2 g of the wood on which the fungus *Ganoderma applanatum* was growing in order to obtain the quantity of nitrogen present in 2.7 g of sporophore tissue or 1.0 g of spores. Studies on the growth of anobiid and cerambycid beetles in decayed wood have shown that the extent of fungal decay significantly affects larval growth (Campbell and Bryant, 1940; Fisher, 1940, 1941; Campbell, 1941; Becker, 1942, 1968, 1977; Bletchly, 1953). The increased feeding rates and reduced developmental times of the larvae result from the physical alteration of the wood structure as well as its nutrient enrichment by the decay fungi.

The role of aquatic hyphomycetes in the chemical and physical conditioning of vascular plant detritus has been well studied. These fungi, characteristic of well-aerated headwater streams, are the initial colonizers of autumn-shed leaves (Bärlocher and Kendrick, 1973a, 1974; Suberkropp and Klug, 1976). Fungal growth brings about softening of the leaf tissue and an increase in the nitrogen content and fungal biomass associated with the decaying leaves. The palatability and nutritional value of these leaves to detritivores such as amphipods and caddisfly larvae increases as a result of these changes (Bärlocher and Kendrick, 1975b; Suberkropp and Klug, 1980; Suberkropp et al., 1983; Arsuffi and Suberkropp, 1984, 1985; Suberkropp and Arsuffi, 1984).

The importance of ambrosial fungi in the nutritional ecology of xyleborine beetles is well documented (Francke–Grosmann, 1967; Norris, 1979). Spores and hyphae of the fungi line the walls of the beetle's gallery and are the major food of both larvae and adults. In the absence of the fungal symbiont, larvae fail to pupate, the oocytes of postdiapause females do not develop, and oviposition does not occur (French and Roeper, 1972, 1975). However, pupation and oocyte development can be restored to a population of aposymbiotic animals if ergosterol is added to the diet (Kok et al., 1970). In a detailed study of *Xyleborus ferrugineus*, Kok and Norris (see Kok, 1979, for references) demonstrated that the sterol metabolism of the beetle and its symbiotic ambrosial fungi are intimately intertwined.

Filamentous fungi are noted for their capacity to secrete copious amounts of stable, extracellular hydrolytic enzymes. This is one of the metabolic traits that makes them so important in the types of substrate conditioning just described. In addition to their evolved function of providing soluble materials for uptake by fungal hyphae, these fungal enzymes can also play an important role in the digestive processes of insects that ingest them (Martin, 1984). Fungal enzymes occur in the gut fluids of fungus-growing ants (Boyd and Martin, 1975a,b), fungus-growing termites (Abo–Khatwa, 1978; Martin and Martin, 1978, 1979), a siricid wood wasp (Kukor and Martin, 1983), and a cerambycid beetle (Kukor and Martin, 1986). In the termites *Macrotermes natalensis* and *M. subhyalinus*, the wood wasp *Sirex cyaneus*, and the beetle *Monochamus marmorator*, fungal carbohydrases are acquired by ingesting fungal tissue associated with the wood that makes up the bulk of the insect's diet. These enzymes persist in the midgut and enable the animals to digest the plant structural polymers that are the insect's major carbon source. Other instances in which acquired fungal enzymes have been implicated in the digestive processes of arthropods involve terrestrial isopods (Hassall and Jennings, 1975), the aquatic amphipod *Gammarus fossarum* (Bärlocher, 1982), and the detritus-feeding aquatic nymphs of stoneflies (Sinsabaugh et al., 1985). Because many detritivores consume mixtures of fungal and plant tissues, it is likely that other examples of an acquired digestive capacity will be found in this group as well as in other wood-feeding species.

## 26.5 ECOLOGICAL AND EVOLUTIONARY ASPECTS

### 26.5.1 Host Specificity among Invertebrates That Feed on Sporocarps

Fungi, in common with herbaceous plants, produce a diverse array of physiologically active secondary metabolites, and effective mechanisms for avoiding or detoxifying these substances would seem to be prerequisite to the effective exploitation of fungi for food. Furthermore, it might be expected that any given fungivorous species would be adapted to deal effectively only with a subset of the allelochemicals represented in the fungal community and hence would restrict its feeding to a subset of chemically similar fungal species. Thus, the chemical diversity and heterogeneity of fungi might be expected to select for specialization among fungivores. However, specialization is a viable strategy only if resources are sufficiently predictable and long-lasting to support an organism through its entire life cycle. The fruiting bodies of fungi are generally ephemeral, variable in abundance, and unpredictable in time and space. Some of the fleshy mushrooms, which may persist for no more than 3–4 days, would seem to be much too unreliable a resource on which to specialize. As a consequence, it might be expected that insects that feed on such ephemeral fungal species would be unselective in their host choice. Thus, fungivorous species are subjected to conflicting selection pressures: chemical diversity selects for specialization, while resource unpredictability selects for generalization.

Numerous faunal surveys of fungal fruiting bodies have revealed varying degrees of specificity in the associations between arthropods and fungal sporocarps. The usual pattern is for an arthropod species to have a range of acceptable fungal hosts that includes some species that are preferred over others. When preferred species are not available, less preferred species may be used heavily. Even arthropod species with very broad host ranges avoid or fail to select many species of fungi. Not surprisingly, the most specific associations involve insects that utilize abundant, predictable, long-lived sporocarps, especially woody polypores that may persist for several years.

The most common beetles found in the fruiting bodies of polypores are members of the Ciidae (Paviour–Smith 1960b; Lawrence, 1973; Gilbertson, 1984). Most ciids prefer to breed in one or two host fungi, but they also occur in several others that are phylogenetically related. A few are reported to be truly monophagous, and a few have very broad host ranges that include as many as 36 fungal species, but no species is indiscriminate. The basis for host acceptability has not been established, although hyphal structure and the physical characteristics of the fruiting body are believed to be important factors. Other important inhabitants of perennial or persistent woody polypores are the mycophagous larvae of tineid moths (Lawrence and Powell, 1969). Some of the tineid species are quite host-specific, but others exploit as many as a dozen different fungi.

The host preferences of the staphylinid beetles of the Gyrophaenina have been thoroughly reviewed by Ashe (1984). The gyrophaenine beetles commonly inhabit polypores and gilled fungi, where they feed by grazing on the spore-bearing hymenium layer. Several patterns of host specificity are evident. Adults may be found on a wide variety of distantly related mushrooms, representing many genera and several families. Although adults of most species may be found on a variety of mushrooms, they are usually more common on members of a few genera. A few species have fairly narrow host ranges, but it is unlikely that any are monophagous. Many fungi are unacceptable to all gyrophaenines, and a few are particularly favored. There are no obvious correlations between the beetles' preferences and the physical or chemical characteristics of the fungi. The beetles occur on species known for their high toxicity to vertebrates as well as on species that are quite innocuous to vertebrates and contain few, or very different, secondary metabolites. Chemical diversity does not appear to have been an insuperable barrier to the evolution of fairly broad host ranges in this family of beetles.

In his study of the insect associates of the Boletales, Bruns (1984) noted that this group of fleshy fungi attracts many more specialists than do the gilled fleshy fungi. In common with gilled fungi, fruiting in the boletes is highly dependent on weather and is therefore seasonably variable and unpredictable. However, because most species of the Boletales are mycorrhizal, their location is fairly predictable. In addition, developmental rates are slow, resulting in sporocarps that persist for comparatively long periods of time. Also, the boletes are generally large, widespread, and abundant, making them a somewhat more reliable and predictable resource than the fleshy, gilled fungi. In any event, seasonal unpredictability has not been a major barrier to the evolution of bolete specialists in the dipteran families Anthomyiidae, Mycetophilidae, Syrphidae, and Muscidae.

Investigations of mycophagous Drosophilidae have addressed a number of questions concerning the ecology and evolution of host selection by fungivorous species. Some species use a variety of short-lived, unpredictable agarics and boletes, whereas others feed on more predictable, longer lived species (Kimura et al., 1977; Jaenike, 1978c; Jaenike and Selander, 1979; Kimura, 1980; Lacy, 1982, 1984a,b). Species that feed on the more predictable mushrooms tend to have narrow host ranges, whereas those using unpredictable species have much broader host ranges. The more specialized species often prefer hosts that are not preferred by the more generalized feeders, whereas the generalists tend to select similar groups of fungal species. Thus, generalists appear to be potential competitors when sympatric.

Indeed, not only have fluctuations in the abundance of generalist species been observed in response to variations in mushroom abundance (Jaenike, 1978a), but reductions in fitness resulting from inter- and intraspecific competition in natural populations have been demonstrated (Grimaldi and Jaenike, 1984). Generalist species accept mushrooms containing an array of different secondary chemicals, providing another demonstration that the chemical diversity of fungi does not necessarily preclude a generalized feeding strategy by fungivores.

In agreement with the niche variation hypothesis, which asserts that a species that uses a variety of resources will exhibit greater genetic variability than one with a more specialized or narrow niche, Lacy (1982, 1984a,b) has demonstrated a significant correlation between electrophoretically detectable variation in various drosophilid flies and the diversity of mushroom species they exploit. However, the occurrence of complete panmixia prevents the evolution of host races (Jaenike and Selander, 1979; Lacy, 1982). As a result, drosophilids with wide host ranges are as polyphagous as individuals as they are as species (Jaenike, 1978b).

### 26.5.2 Host Specificity among Invertebrates That Feed on Materials Colonized by Fungi

Many species of invertebrates coexist on the same detrital substrate in aquatic ecosystems, and it is becoming increasingly evident that the fungi associated with detritus play a major role in determining how resources are partitioned among similar coexisting species. Detritus is a coarse-grained resource, the heterogeneity being introduced by the diversity of plant material serving as substrates, the multiplicity of fungal species that colonize these substrates, temporal variability, and changes brought about by invertebrate feeding.

The larvae of caddisflies (Trichoptera), which are important shredders of aquatic detritus, are able to discriminate between and selectively feed upon leaves colonized by different fungi, or upon patches of different fungi on the same leaf (Arsuffi and Suberkropp, 1984, 1985). The three caddisfly species studied, which are not potential competitors because they are abundant at different times during the year, exhibit similar preferences among the fungi or fungus-colonized leaves. By contrast, larvae of two species of mayflies (Ephemeroptera), which are potential competitors owing to their temporal and spatial coexistence, exhibit very low overlap in feeding preferences (Bassett and Rossi, 1982a,b). In these two species, leaf pack selection is dictated mainly by the fungi present on the leaves rather than by the leaf species serving as substrate.

In a comprehensive study, the trophic niches of two species of detritus-feeding aquatic isopods were compared in areas of sympatry and allopatry (Rossi and Fano, 1979; Rossi et al., 1983; Rossi, 1985). In both species, the palatability of the detritus is determined by microfungi present on the substrate. In allopatry, the two isopod species have similar trophic niches, preferentially selecting and surviving best on detritus colonized by the same species of fungi. In sympatry, however, there is considerable divergence in the trophic niches of the two species. Each selects and survives best on detritus colonized by different sets of fungi. Furthermore, the fungi preferred by allopatric populations are the most common ones in the habitat, whereas the fungi preferred by sympatric populations are the less abundant ones. The case for character displacement seems strong. It was also demonstrated that each population was polymorphic in terms of its metabolic and behavioral characteristics because of the presence of diverse genotypes with different trophic needs and metabolic capacities.

An interesting example of the importance of yeasts in determining habitat suitability is provided by cactophilic *Drosophila* of the Sonoran desert (Fogelman et al., 1981). *Drosophila mojavensis* is an ecological generalist, colonizing a variety of cactus species. This wide host range may be possible because the larvae are yeast specialists, seeking out parts of the cactus supporting the widely distributed cactus yeast, *Pichia cactophila*. By contrast, other cactophilic *Drosophila* appear to be ecological specialists restricted to a much narrower range of cactus species, but yeast generalists that accept whatever yeasts may be present on their host.

## 26.6 CONCLUSIONS

This chapter has emphasized the varied circumstances under which the consumption of fungal tissue occurs and the diverse questions that can be addressed through the study of the nutritional ecology of fungus feeders. Fungal tissue is the exclusive or primary food of many species, and the study of mycophagy provides opportunities to probe fundamental questions concerning evolutionary, ecological, and biochemical aspects of the interactions of consumers with their food. In addition, fungi are significant third parties in the nutritional interactions of many invertebrate species with substrates of plant origin, such as detritus, foliage, wood, roots, seeds, fruits, and stored agricultural products. Studies of the role of mycophagy in these systems promise to generate insights that are not only of fundamental importance but also of practical significance to industry, agriculture, and public health.

Mycophagy has not received the attention that its wide-ranging significance would seem to warrant. At the present time it is a field ripe for development, and its future directions are likely to be determined by investigators with quite varied perspectives.

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